A New Phyllolepid Placoderm Occurrence (Devonian Fish) from the Dulcie Sandstone, Georgina Basin, Central Australia

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A new phyllolepid placoderm occurrence from a low level in the Dulcie Sandstone, Georgina Basin, Northern Territory, lies about 200 metres stratigraphically above an older fish assemblage containing *Wuttagoonaspis*. A new species *Austrophyllolepis dulciensis* is characterised by an unusually broad anterior ventrolateral plate. The stratigraphic range of other species in this genus from southeastern Australia and Antarctica suggest a Givetian-Frasnian age. Early members of the order Phyllolepida are endemic to east Gondwana, and other phyllolepids of similar age occur in Turkey and Venezuela. In the Northern Hemisphere (Europe, Russia, Greenland, North America) phyllolepids are restricted to the latest Devonian stage (Famennian). This disjunct space-time distribution for the group supports a Gondwanan origin for the Phyllolepida, and later access to northern landmasses resulting from closure of the ocean between Gondwana and Laurussia at or near the Frasnian-Famennian boundary.

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KEYWORDS: Devonian, Georgina Basin, Phyllolepida, Placoderm fishes.

INTRODUCTION

Devonian fossil fish remains from central Australia were first documented by Hills (1959), who identified the placoderm genera *Bothriolepis* and *Phyllolepis* and concluded a Late Devonian age for the Dulcie Sandstone in the Dulcie Range, N.T. (Georgina Basin; Fig. 1). An older fish assemblage from the basal part of the Dulcie Sandstone at the northwestern end of the Dulcie Syncline was discovered during geological mapping by the Bureau of Mineral Resources in 1961. Further material was collected by the author from these and many new localities during two field trips to the Georgina Basin (1974, 1977). The entire fauna of the lower assemblage, including a new species of the genus *Wuttagoonaspis* Ritchie (1973), has been described by Young and Goujet (2003). Ten new localities in the lower part of the Dulcie Sandstone were documented, of which six (localities GY74/8-13) were collected in 1974 along the southern flank of the Dulcie Range on the southeastern edge of the Barrow Creek 1:250 000 sheet (Fig. 1B). There were no taxa in common with the earlier descriptions of Hills (1959) and Young (1985, 1988), which dealt with younger fish assemblages from the upper part of the Dulcie Sandstone (localities GY1-7 of Young 1988: fig. 4). A diagnostic group in these younger assemblages are the phyllolepid placoderms.

The specimens described in this paper were collected from one of the localities (GY74/8) documented by Young and Goujet (2003). Initially they were put aside as unidentified smooth mudclast impressions in sandstone. However, the shape of bones now clearly demonstrates that the sample represents impressions of bones belonging to a phyllolepid placoderm. Some 19 genera representing 13 taxa of family or higher rank have been documented by Young and Goujet (2003) in the *Wuttagoonaspis* Assemblage, which is known from localities over about one million square kilometres of the Australian continent. However, phyllolepid placoderm remains have never been confirmed in that assemblage. This

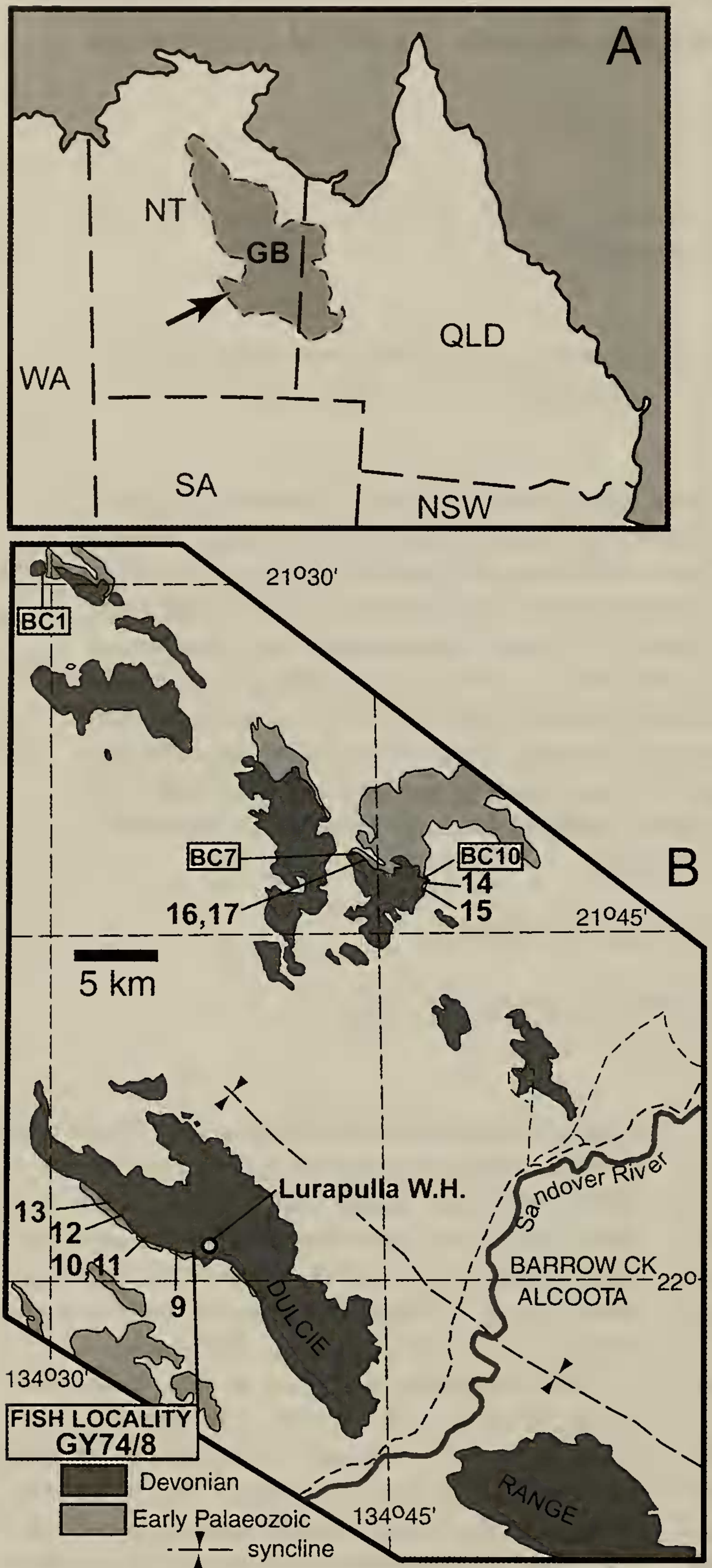

Figure 1. A, location of the Dulcie Range, on the southwestern flank of the Georgina Basin (GB) in northern Australia. B, Fossil fish localities in the northwestern part of the Dulcie Syncline, with geology generalised from the Barrow Creek and Alcoota 1:250 000 sheets (modified from Young and Goujet 2003: fig. 1). The samples described herein come from locality GY74/8.

new phyllolepid occurrence is significant in coming from an intermediate level in the Dulcie Sandstone, all previous examples of phyllolepids (Hills 1959; Young 1988) coming from near the top of the sequence.

Phyllolepids, like *Wuttagoonaspis*, have dermal bones with ridged ornament. Before *Wuttagoonaspis* was described by Ritchie (1973), all fish remains with ridged ornament from the Australian Devonian were referred to *Phyllolepis* without question (e.g. Rade 1964). In Europe *Phyllolepis* is only known from the youngest stage of the Late Devonian (Famennian), and on this basis all such occurrences in Australia were originally assigned to the Famennian (e.g. Hills 1929, 1931). But Hills (1958) also noted that the temporal significance of different placoderm genera in the Upper Devonian of Europe did not apply in Australia, and Young (1974) demonstrated that some phyllolepid occurrences were older (Frasnian) than in Europe. Some authors (e.g. Ritchie 1973) considered the phyllolepids and *Wuttagoonaspis* to be only distantly related, and recently Dupret (2004) has regarded the ridged ornament as a non-homologous character. The alternative hypothesis (e.g. Miles 1971; Young 1980; Long 1984; Young and Goujet 2003) is that ridged ornament is a shared derived feature, which with some others indicates that *Wuttagoonaspis* and phyllolepids are sister groups. Apart from ornament, the shape of bones is quite different in the two taxa, so impressions with ridged ornament can be readily assigned to one or the other group if bone margins are complete. Thus, examination of the ridged fragment called *Phyllolepis* by Gilbert-Tomlinson (1968) showed clearly that it belongs to *Wuttagoonaspis* (Young and Goujet 2003, fig. 3E). Similarly, impressions of the inner unornamented surface described below can unequivocally be assigned to a phyllolepid on the basis of bone shape.

Locality

Fossil fish localities GY74/8-13 along the southern flank of the Dulcie Range (Fig. 1B) supposedly came from the basal 10 m of the Dulcie Sandstone (Haines et al. 1991: 32), but poor outcrop, and some material collected from scree, make the actual interval of occurrence difficult to establish (Young and Goujet 2003). The boundary with the underlying Tomahawk beds (Cambro-Ordovician) is variously interpreted, as a faulted contact on the second edition of the Barrow Creek 1:250 000 geological map (Haines et al. 1991) but as a disconformity on the adjacent Huckitta map sheet (Freeman 1986).

The most easterly of these fish occurrences (GY74/8, Figure 1B) is recorded in field notes as being immediately above the contact with the underlying Tomahawk beds and was the first at which fish remains were discovered by the author in the lower Dulcie (on 7 July 1974). This is the locality yielding the specimen described below. Locality 74/8 was about 800 m west of the field campsite at Lurapulla Waterhole.

Stratigraphic level

The samples were labelled 'top of Dulcie; collected 7/7/74'. According to field diary records only locality 74/8 was visited on that day, when the adjacent section through the Dulcie Sandstone was also examined. Stereo air photos of locality 74/8 (Barrow Creek 17-10-70, run 9, photos 0025, 26) show the highest elevation in the vicinity of two ridges about 1 and 1.8 km to the NW, where beds have a very shallow dip (5° on the Barrow Creek geological sheet, first edition). Lower beds are more inclined, with a dip of 16° marked on the second edition geological map just above Lurapulla Waterhole. Estimates based on air photo interpretation suggest that the samples described below came from an interval about 200+ m above the fish horizon at the base of the sequence. At locality 74/8 the basal level yielded only indeterminate phlyctaenioid arthrodire remains (impressions with tuberculate ornament). However, another locality along strike about 3 km to the NW (74/11) produced some 50 samples belonging to seven taxa, including *Wuttagoonaspis* (Young and Goujet 2003: table 1). At none of the 26 localities covered in that study were phyllolepid remains identified. It was concluded that younger bothriolepid-phyllolepid placoderm assemblages did not occur in the lower part of the Dulcie Sandstone, nor in the Cravens Peak Beds (*contra* Gilbert-Tomlinson 1968, and Draper 1976). However, they are recorded from the upper part of the Dulcie Sandstone at the southeastern end of the Dulcie Range (about 490 and 600 m above base; Young 1988), where the type section records a thickness of 621 m. These horizons occur in sandstone mesas in the core of the syncline, representing the upper subdivision of the formation and are separated by valleys of recessive strata from more prominent outcrops of the lower Dulcie Sandstone (e.g. Freeman 1986, pl. 20).

Freeman (1986) identified the upper and lower facies in the vicinity of the type section but dismissed the suggestion (Gilbert-Tomlinson 1968) of a possible paraconformity within the lower unit. He noted a decrease in thickness to an estimated 250 m in the northwestern exposures on the Huckitta sheet. No sections were measured by Haines et al. (1991) on the Barrow Creek sheet, but the Dulcie Sandstone is much thinner (30-40 m) on the Elkedra sheet to the north-west (Stidolph et al. 1988).

A question arises as to whether the thinning of the Dulcie is general throughout the sequence or whether the lower or upper part is missing from the thinner stratigraphic sections. As first noted by Gilbert-Tomlinson (1968), the lower and upper fish assemblages in the Dulcie generally do not occur together. The occurrence reported here is the only one known so far that represents two distinct fish faunas within the same section. Previously (Young 1985: 251) a stratigraphic thickness of about 430 m was estimated between the lower *Wuttagoonaspis* and upper *Bothriolepis – Phyllolepis* fish assemblages, but the new fossil sample described below comes from some 200 m above the lower fish horizon. Decrease in thickness to the north-west from the type section would place this new phyllolepid occurrence near the top of the formation as exposed on the Barrow Creek sheet. If it correlates with those from the SE it could be assumed that the middle recessive part of the Dulcie Sandstone in the type section has been lost, retaining two distinct fish assemblages with no taxa in common within a section some 200-300 m thick. It is considered more likely that it represents a lower phyllolepid assemblage, given that a rather diverse fauna of unknown biostratigraphic relationship is indicated from fragmentary remains already described (Young 1988). Comparison can be made with the Pertnjara Group in the Amadeus Basin, where thickness extrapolations suggest a separation between the assumed level for the *Wuttagoonaspis* fauna in the base of the Deering Siltstone Member and the *Bothriolepis* assemblage within the Harajica Sandstone Member to be about 280 m at Stokes Pass, and possibly as low as 100 m at Dare Plain (Young 1985: 251, 252). A new species of the phyllolepid *Placolepis* has recently been described from the Harajica fish assemblage (Young in press a).

ABBREVIATIONS

Measurements of total length (L), breadth (B), length of the anterior division of the AVL (L_{AD}), and level of the lateral corner (lc) of the PVL (as a percentage of total length) are summarised in Figure 3 (below). Bone proportions are given as a ratio of breadth to length expressed as a percentage (abbreviated as 'B/L index'). Standard abbreviations for placoderm dermal bones and other structures are used in the text and figures as follows:

ADL, anterior dorsolateral plate;
AL, anterior lateral plate;
AMV, anterior median ventral plate;
AVL, anterior ventrolateral plate;
cf.IL, contact face overlapping interolateral plate;
cf.SP, contact face overlapping spinal plate;
IL, interolateral plate;
lc, lateral corner;
m.AMV, margin abutting anterior median ventral plate;
m.PMV, margin abutting posterior median ventral plate;
oa.AVL, area overlapped by AVL plate;
pect, pectoral embayment (margin) of AVL plate;
PMV, posterior median ventral plate;
PNu, paranuchal plate;
PVL, posterior ventrolateral plate;
ppec, prepectoral corner;
ptpec, postpectoral corner;
SP, spinal plate.

SYSTEMATIC PALAEONTOLOGY

Class PLACODERMI McCoy, 1848
Order PHYLLOLEPIDA Stensiö, 1934

Diagnosis

Placoderms in which the nuchal plate is much enlarged, as broad or broader than long, and surrounded by five smaller paired bones including paranuchal, marginal, postorbital and preorbital plates. Paranuchal plate with well-developed postnuchal process, and rostral, pineal, and central plates absent from skull roof. Trunk armour relatively broad; median dorsal plate lacks an inner keel; anterior dorsolateral plate with narrow elongate exposed area; anterior ventral and posterior lateral plates absent; posterior dorsolateral and anterior and posterior median ventral plates reduced or absent. Anterior ventrolateral plates short and broad, and posterior ventrolaterals triangular, with ossification centres near anteromesial corners; both ventrolateral plates relatively flat, lacking a lateral lamina, and meeting in part or all of the midline in non-overlapping sutures. Dermal ornament mainly of smooth concentric ridges, with some tubercles and tubercle rows.

Remarks

The diagnosis provided by Ritchie (1984: 344) was slightly reworded from that of Denison (1978: 41), and included reference to the absence of rostral and pineal plates from the skull, used by Denison to separate his two suborders 'Antarctaspina' and 'Phyllolepina'. *Antarctaspis* is now regarded as an actinolepid related to *Toombalepis* and *Yujiangolepis*, which also have converging sensory grooves on the nuchal plate (Young and Goujet 2003: fig. 16), a primitive feature and not a criterion for indicating close relationship to phyllolepids. Ritchie (1984: 346) gave an additional diagnosis for the family Phyllolepidae that combined features of Denison's subordinal and family diagnoses, but there are no good criteria for grouping genera within the order at this stage.

The above diagnosis excludes characters that are evidently primitive by outgroup comparison (e.g. converging sensory canal grooves on the skull, median dorsal plate short and broad and lacking inner keel, sliding dermal neck-joint). New characters include features of the trunk armour bones typical of the group. The much reduced external part of the anterior dorsolateral (ADL) plate is a condition approached in *Bryantolepis*, *Kujdanowiaspis* (Denison 1958: fig. 108) and *Wuttagoonaspis*. The anterior ventrolateral (AVL) is relatively broad compared to that of other primitive arthrodires, in which the posterior ventrolateral (PVL) has complex midline overlaps, and a prominent lateral lamina (Denison 1958: figs. 112, 114). The ossification centre of the PVL is normally placed laterally near the posterior end of the lateral lamina (e.g. *Actinolepis*; Mark-Kurik 1973: fig. 13), but its anteromesial position in phyllolepids is well shown by the concentric ornament of *Austrophyllolepis* (Long 1984: fig. 11D). New phyllolepids from southeastern Australia show that the posterior dorsolateral (PDL) plate is retained in some members of the order (Young, in press b), although it is lost in *Phyllolepis*, *Austrophyllolepis*, and probably *Placolepis* (Long 1984; Ritchie 1984).

Genera included in the family and order are *Phyllolepis*, *Austrophyllolepis*, and *Placolepis*, plus two new phyllolepid taxa from southeastern Australia (Young in press b). The genus *Pentagonolepis* Lohest, 1888, from the Famennian of Belgium, was synonymised with *Phyllolepis* by Leriche (1931), Stensiö (1939) and Denison (1978). However, the ridged ornament on the nuchal plate from the skull roof, on which the species *Phyllolepis (Pentagonolepis) konincki* is based (Stensiö 1939, fig. 6B), suggests a rounded anterior margin (incomplete), somewhat similar to the corresponding bone of *Placolepis* described by Ritchie (1984). The Belgian specimen differs from *Placolepis* in that the middle pitline is directed towards the lateral corner of the plate, as in *Phyllolepis*, rather than well behind that corner. It seems likely that the paranuchal plate from the same skull had extensive contact with the postorbital plate. Restudy of this material, and any new specimens from Belgium, is needed to confirm the shape of the nuchal, but '*Pentagonolepis' konincki* Loheste, 1888 could be a valid taxon, morphologically intermediate between *Placolepis* and *Phyllolepis* in the configuration of skull bones. It is noted that the first Devonian tetrapods from continental Europe have recently been described from these localities, in the Evieux Formation of Belgium (Clément et al. 2004).

Austrophyllolepis **Long, 1984**

Diagnosis

Phyllolepids in which the sensory groove passes off the paranuchal plate in the anterior third of plate length, and the external surface of the marginal plate is similar in breadth and length, with the postmarginal sensory canal junction in about the middle of plate length. A small suborbital plate is articulated to an ossified process below the postorbital plate, and the submarginal plate may be ossified. The trunk armour has a posterior median ventral plate that forms a distinct notch in the mesial margins of anterior and posterior ventrolateral plates. The ridged ornament includes extensive areas of tuberculation and some ridge duplication.

Austrophyllolepis dulciensis **sp. nov.**

Name

Shortened from 'Dulcie', after the type formation and locality (Dulcie Sandstone and Range, Georgina Basin, Northern Territory).

Diagnosis

A species of *Austrophyllolepis* in which the anterior ventrolateral plate is as broad as long (breadth/length index about 100), with anterior and posterior divisions about 20% and 30% of total length and a slightly concave spinal margin; posterior median ventral plate elongate and free part of spinal plate relatively short.

Remarks

The generic diagnosis from Young and Long (in prep.) is updated from Long (1984). Most of the characters are not observable in the material described below, but the evidence of a posterior median ventral (PMV) plate in the trunk armour is the criterion for referring the species to *Austrophyllolepis* (see further comments below). Characters in the specific diagnosis separate the new species from previous species of *Austrophyllolepis*. The unusually broad anterior ventrolateral (AVL) plate distinguishes *A. dulciensis* sp. nov. from all previously described phyllolepids in which this plate is known.

Material

ANU V3064 (holotype; associated AVL, PVL and SP plates); ANU V3065 (incomplete PVL plate), both preserved as impressions in hard sandstone.

Locality and Horizon

Locality GY74/8, southern flank of Dulcie Range (Fig. 1B), from a horizon about 200 m above the exposed base of the Dulcie Sandstone (see Young and Goujet 2003: 5 for locality details).

Description

The impressions of closely associated phyllolepid trunk armour plates comprise an almost complete right AVL plate, overlain by a SP plate and a right PVL plate (Fig. 2A). Another AVL is separated by 45 mm from the first (Fig. 2B), and an incomplete left PVL impression is preserved on the second smaller sandstone sample (ANU V3065). The two AVL plates (termed AVL#1, AVL#2) were first assumed to be internal impressions of left and right plates from one individual, because both appeared to lack ornament. Closer examination showed that both are right plates. The second specimen (AVL#2; Fig. 2B) is slightly convex rostrocaudally, and must have been an external surface impression, even though it is smooth. A new phyllolepid genus with smooth dermal bones has recently been documented from southeastern Australia (Young, in press b). However, in ANU V3065 absence of ornament may be a post-mortem effect due to 'sand-blasting' in a river current removing the ridged ornament from most of the external surface. Short sections of relatively coarse ridges are retained on the downturned posteromesial and spinal margins of the bone (ri, Fig. 2B), presumably protected from abrasion beneath the sediment-water interface. The relatively flat ventral plates of the phyllolepid trunk armour would have made them hydrodynamically stable with either external or internal surfaces uppermost, in contrast to some other common placoderm remains, for example the strongly angled trunk armour bones of the widespread antiarch *Bothriolepis*.

The anterolateral and prepectoral corners of AVL#2 are incomplete, and the posterolateral part is missing off the edge of the sample. This and the first AVL clearly came from two individuals of about the same size, and shape differences are assumed

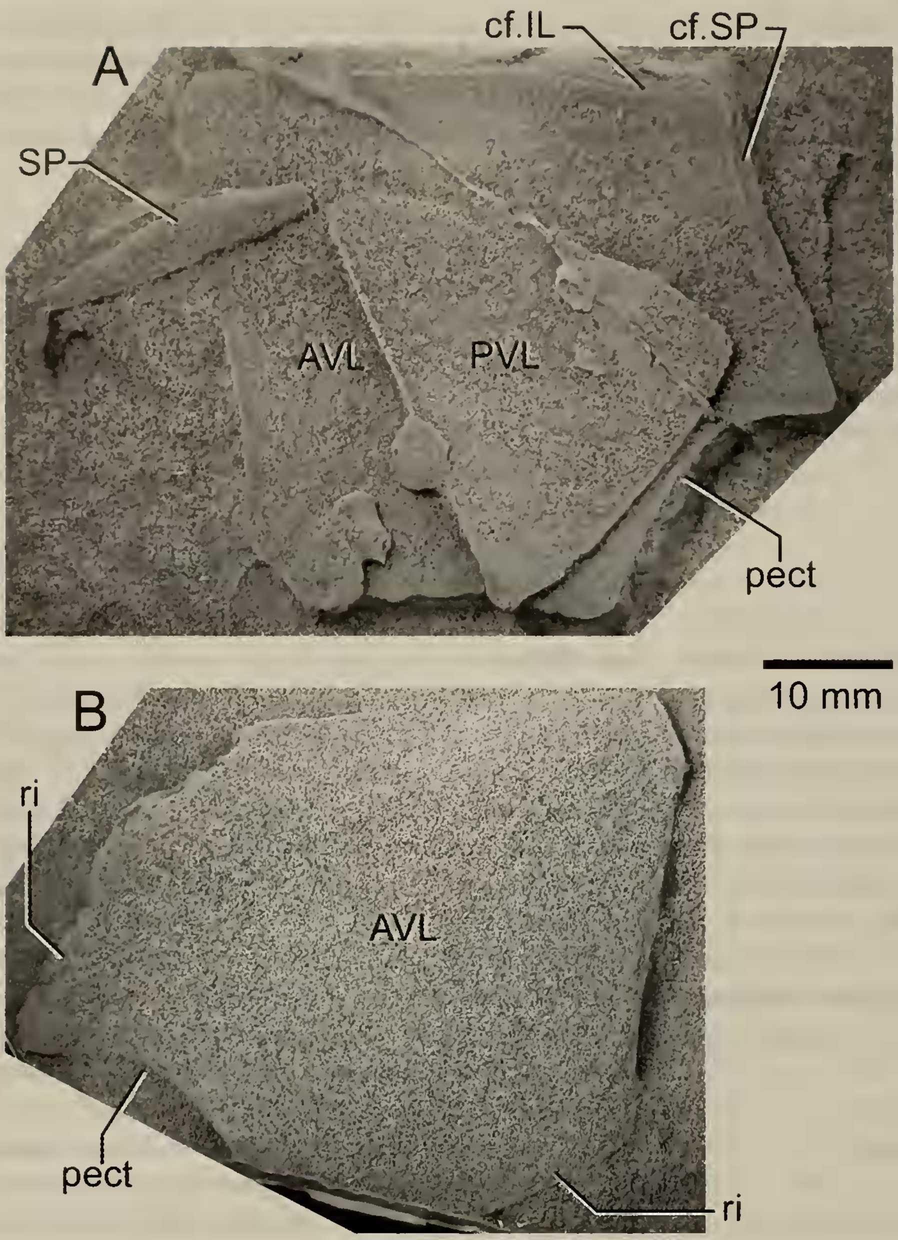

Figure 2. ANU V 3064 showing associated AVL, PVL and SP plates of *Austrophyllolepis dulciensis* sp. nov. (A), and the second AVL plate (B). Both are latex casts of sandstone impressions whitened with ammonium chloride.

to be intraspecific variation, given the very similar proportions of the two restored plates (see below). AVL#1 (Fig. 2A) exposes the visceral surface, which is gently concave rostrocaudally, with the anterior margin curved up, forming a slight rim mesially. Around the anterolateral corner a second ridge inside the margin defines a narrow contact face for the IL and SP plates (cf.IL, cf.SP, Fig. 2A, 3A). A diagonal groove crosses the visceral surface of the AVL in *Placolepis* (Ritchie 1984: fig. 11A-B) and is a distinctive feature of that genus. It is not developed in the Victorian material of *Austrophyllolepis* (Long 1984, 1989) and is absent in this new specimen. The spinal margin, which in all other phyllolepid taxa is convex, in this AVL is gently concave anteriorly and straight posteriorly (Fig. 3A). The mesial margin, normally straight in phyllolepids, is slightly convex anteriorly and concave posteriorly, again showing the raised rim typical of phyllolepid AVL plates where they form a non-overlapping suture in the midline. In that case the margin must be straight, but AVL#1 indicates a gap in the midline for a small PMV plate, as in *Austrophyllolepis* from Victoria (Long 1984: fig. 11D). In AVL#2 the preserved spinal margin and the posterior part of the mesial margin are also gently concave (Fig. 2B), as in AVL#1. Reconstruction (Fig. 4), based on AVL#2, suggests that the Dulcie Range species must have had a larger PMV than in the Victorian species. Of these, *A. ritchiei* had the longer PMV (Long 1984: figs. 7B, 13B) but with a concave external margin (convex in the new specimens). There is a distinct short posteromesial margin on AVL#1 (m.PMV, Fig. 3A), occasionally seen in other species (e.g. interpreted as a broken edge in *Phyllolepis concentrica* by Stensiö 1939: fig. 1).

AVL#2 differs in lacking a posteromesial margin, but has an anteromesial margin defined by distinct corners (m.AMV, Fig. 4). Ritchie (1984: 342-3) assumed the AMV to be absent in European *Phyllolepis* and in *Placolepis*, as did Long (1984) for *Austrophyllolepis*. One specimen assigned to *A. youngi* does suggest an anterior median element (Long 1984: fig. 18C), as in *Phyllolepis woodwardi* from Europe (Stensiö 1939: fig. 2). An AMV plate is also present in a new phyllolepid taxon from Merriganowry, N.S.W. (A. Ritchie, pers. comm.). Since both AMV and PMV plates were primitively present they would be expected to be variably developed in basal phyllolepid taxa (for example the two PMV plates in Victorian material; Long 1984: fig. 6).

Both AVLs as restored are as broad as long (B/L

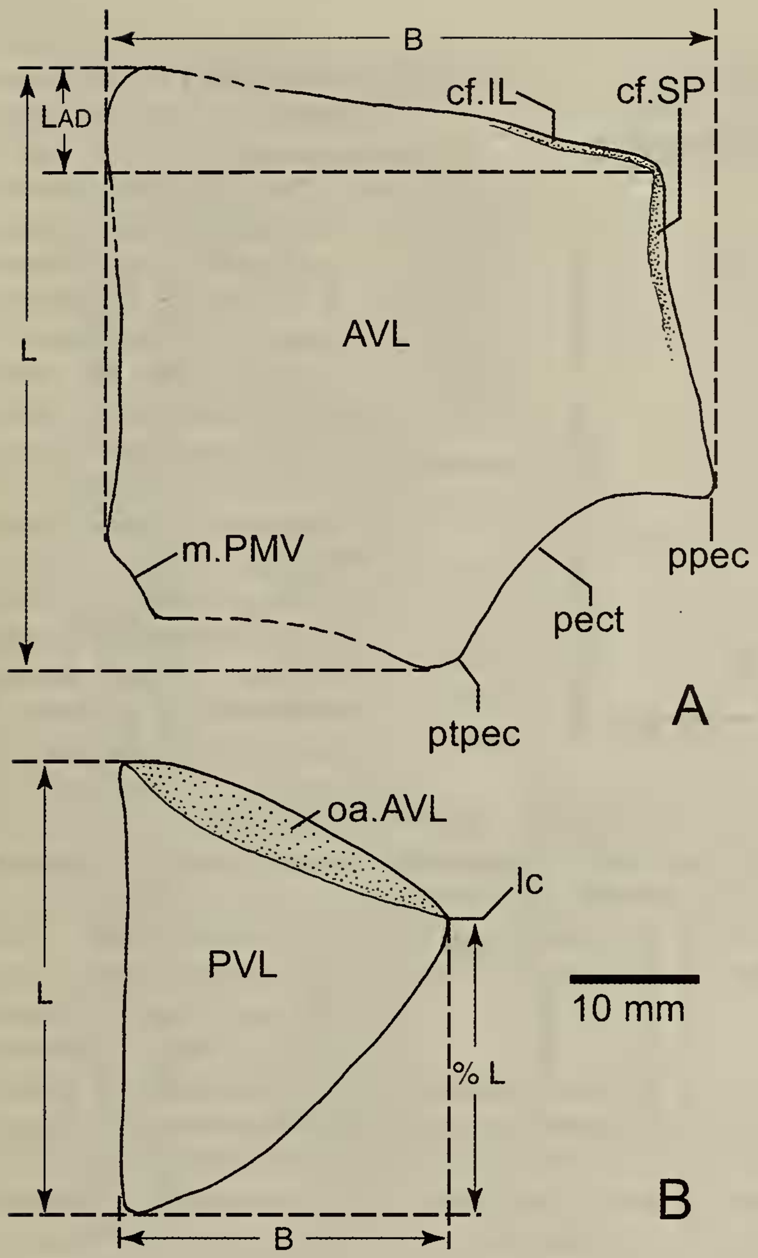

Figure 3. ***Austrophyllolepis dulciensis*** **sp. nov. A, AVL plate of Fig. 2A (AVL#1) slightly restored. B, PVL plate of Fig. 2A, restoration of external surface. ANU V3064.**

index 100), with a similar length of the anterior division (19-20%). In contrast, in both *Austrophyllolepis* and *Placolepis budawangensis* (Long 1984; Ritchie 1984: fig. 11), and all species of *Phyllolepis* from Europe (Stensiö 1939), the AVL is consistently longer than broad. Since the precise measurements for the AVL as summarised in table form by Stensiö (1939: 7) were not clearly defined, measurements used here are indicated in Fig. 3.

The main difference in the two AVLs described here is the orientation of the posterior margin, giving a greater posterior angle (~78°) in AVL#1 than in AVL#2 (~60°), the latter approximating to the anteromesial angle of the PVL (~65°). Distortion in the specimens is discounted because the anteromesial angle of the AVL is much the same in both (75-80°).

The complete PVL impression shows the visceral surface of a left plate (Fig. 2A), with a raised inner rim along its straight mesial margin (L 33 mm) which abutted against the right PVL. A thickened zone inside the anterior margin probably reflects the position of the overlap area for the AVL on the external surface (oa.AVL, Fig. 3B). The B/L index (73) places this PVL at the broader end of the variation for *Placolepis budawangensis*, which is broader than in *Austrophyllolepis edwini*, *A. youngi* and three European species (*Phyllolepis orvini, Ph. nielseni, Ph. tolli*), but more narrow than in *A. ritchiei* (Young 1988: table 1), with *Austrophyllolepis* differing from the other taxa in the more posterior level of the lateral corner (Long 1984: fig. 7; 1989: fig. 4). The shape and proportions of the PVL described here are also notably different from the two PVLs from the Amadeus Basin (Young 1988: table 1). The second incomplete PVL (ANU V3065) shows the mesial margin of a right plate impression, also 33 mm long, and thus perhaps from the same individual.

The complete PVL of Fig. 2A does not fit properly against the underlying AVL, but makes a good fit with AVL#2, so these were used for the reconstruction (Fig. 4). The associated SP plate impression is missing both ends, but restored length is about 33 mm. The distal 4 mm of the preserved part has a closed posterior margin, with the bases of about 4 denticles preserved on what is assumed to be the ventral margin. This margin shows a slight angle in the middle of the preserved part, assumed to fit into the concave margin on the AVL. The opposite lamina (presumed to be dorsal) is more rounded. This SP plate cannot be restored with the free part of the spine as long as in *Placolepis*, or in the Victorian *Austrophyllolepis* (33% and 25% of total length respectively; Ritchie 1984: 342; Long 1984: 272). However, in *Phyllolepis orvini* the free part of the SP plate is much shorter (Stensiö 1936: fig. 20).

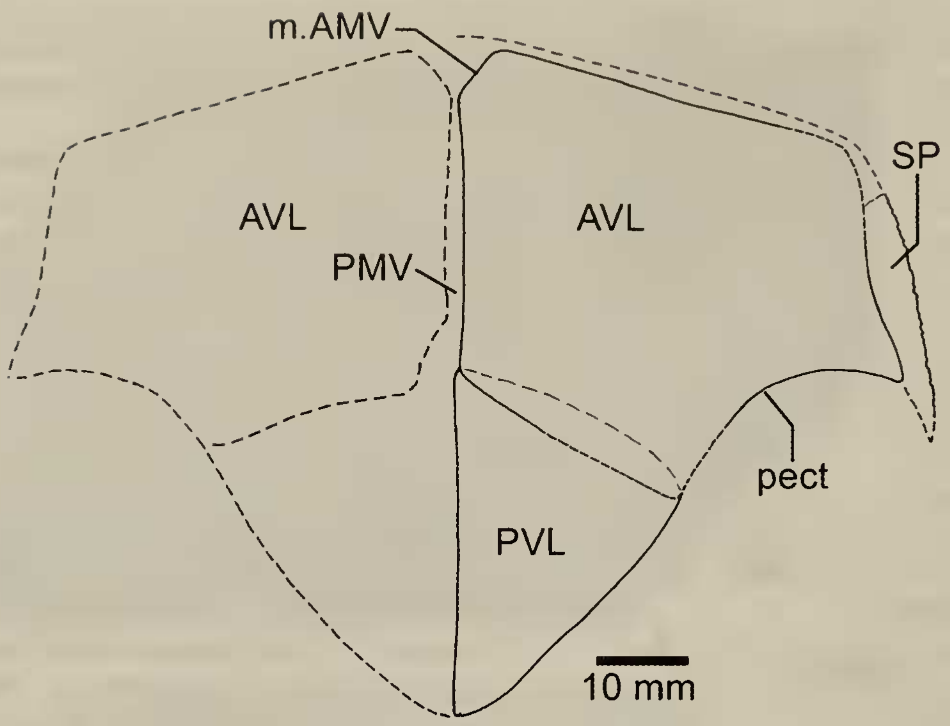

Figure 4. *Austrophyllolepis dulciensis* sp. nov. Attempted restoration of ventral trunk armour; outline shape, and plates of the right side based on the AVL plate of Fig. 2B (AVL#2), and the PVL plate of Fig. 2A; left side indicates the shape of AVL#1 (Fig. 2A); gap left for the PMV plate suggests a variable shape in this species (PMV).

DISCUSSION

These few phyllolepid remains are apparently 'primitive' compared to *Phyllolepis* in Europe by showing evidence of a PMV plate of appreciable size, a character by which they can be referred to *Austrophyllolepis* Long, 1984. However, they differ from all three species of the genus so far described (Long 1984, 1989). It is unclear how reliable the criterion of PMV presence will prove as a generic character, since both AMV and PMV were presumably present in phyllolepid ancestors and their reduction and loss may have occurred independently in different lineages. For the present this criterion is retained to allocate this species to the genus *Austrophyllolepis*. Although the ridged ornament is not preserved, the distinctive triangular PVL plate clearly places these impressions within the Phyllolepida as defined above. In other arthrodires, and in *Wuttagoonaspis* (e.g. Young and Goujet 2003: fig. 8G), the PVL has a distinct lateral lamina, the primitive condition. The loss of this lamina, giving an essentially flat bone, may account for the fact that impressions of the phyllolepid PVL are more commonly found than other bones of the trunk armour, because its hydrodynamic qualities would have resembled those of a flat mud clast.

The fact that this phyllolepid evidently came from a horizon some 200+ m stratigraphically above a completely different fish assemblage, which lacks phyllolepids but contains the possible primitive sister group *Wuttagoonaspis*, might suggest that this is a relatively early phyllolepid occurrence. In a comparison of stratigraphic thicknesses between fish horizons across central Australia, Young (1985: fig. 10) concluded that the previous Dulcie Range phyllolepid occurrences could be somewhat younger than the phyllolepid – bothriolepid occurrences in the Harajica Sandstone of the Pertnjara Group in the Amadeus Basin. This new description of probable *Austrophyllolepis* sp. lower in the Dulcie sequence suggests that the diversity of phyllolepids in central Australia is greater than previously thought, as is now demonstrated in southeastern Australia (Young, in press b) and Antarctica (Young and Long submitted). By comparison with species of both *Austrophyllolepis* and *Placolepis* in southeastern Australia, the age of the lower phyllolepid occurrences in central Australia can be assumed to lie within the Givetian-Frasnian interval. Recent work on the age of the Mount Howitt fish assemblage within the Middle-Late Devonian volcanics of eastern Victoria, the type locality for *Austrophyllolepis*, supports a late Middle Devonian age on both palaeontological and isotopic evidence (Long 1999; Compston 2004).

The diversity of phyllolepid taxa in East Gondwana, and their earlier occurrence than in the Devonian of the Northern Hemisphere, supports the hypothesis of a Gondwanan origin for the group, followed by dispersal into Laurussia in the Famennian resulting from palaeogeographic change at or near the Frasnian-Famennian boundary (Young 1989, 1990, 1993b, 2003). A summary of biostratigraphic ranges (Fig. 5) shows diverse phyllolepids in the Givetian-Frasnian of East Gondwana, with related forms in the largely endemic *Wuttagoonaspis* assemblage (Young

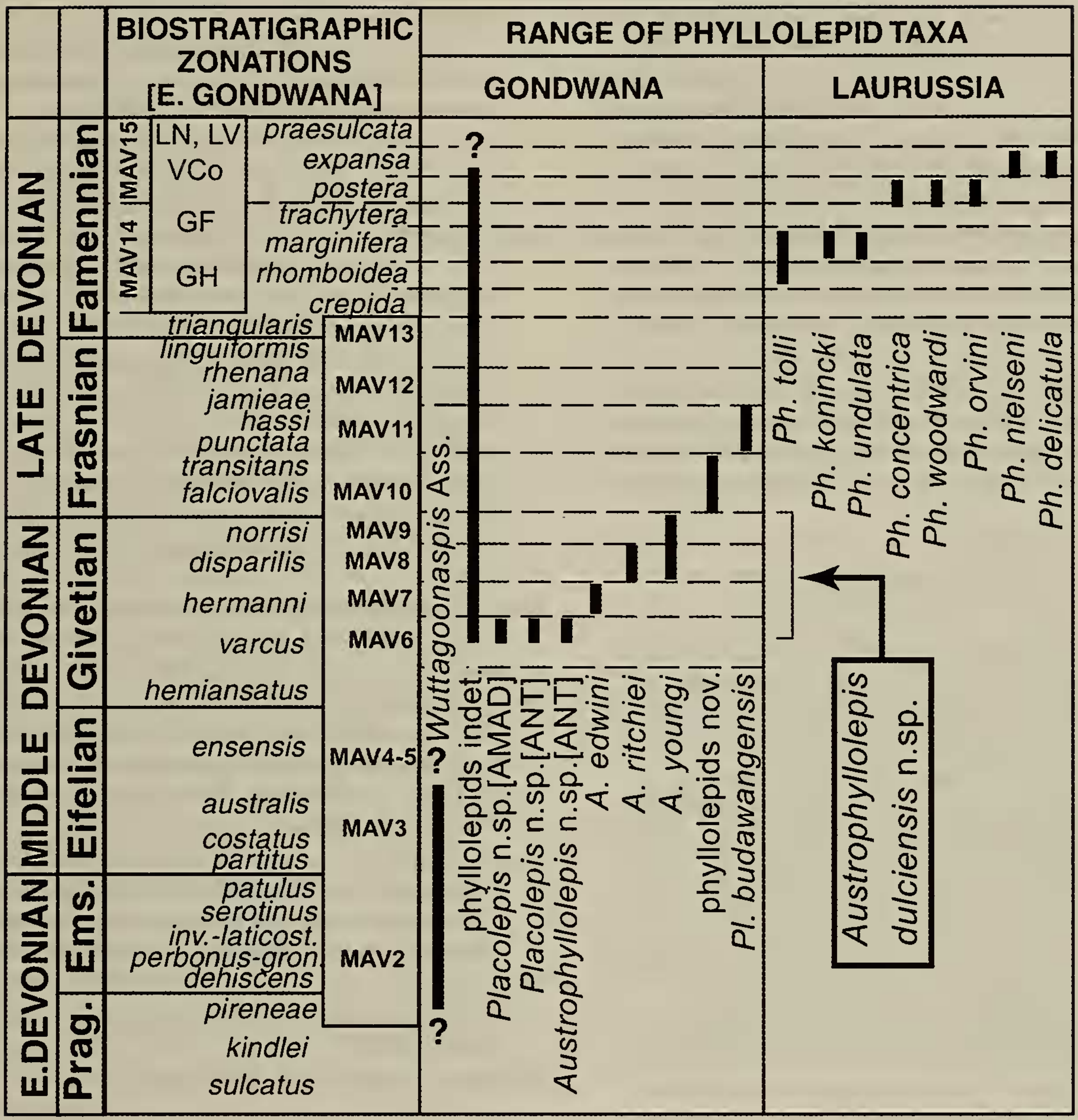

Figure 5. Summary of known stratigraphic ranges (?Pragian-Famennian) for wuttagoonaspids-phyllolepids in East Gondwana (Australia, Antarctica), and the genus *Phyllolepis* in Laurussia (ANT= Antarctica; AMAD= Amadeus Basin). Approximate interval for *Austrophyllolepis dulciensis* sp. nov. from the Dulcie Sandstone indicated, based on the range of other species of the genus. Australian stratigraphic range data updated from Young (1993a: fig. 9.3) and Young (1999: fig. 5). Conodont zonation after Talent et al. (2000). Approximate alignment of macrovertebrate (MAV), miospore (GH, GF, VCo, LN, LV), and conodont zones modified from Young (1996) and Young and Turner (2000).

and Goujet 2003) probably extending down into the Early Devonian, some 22 conodont zones before species of the genus *Phyllolepis* are documented in the Northern Hemisphere (in the Famennian *rhomboidea* conodont zone). This disjunction in time and space is an outstanding feature of global distribution patterns amongst Devonian fishes.

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REFERENCES

Clément, G., Ahlberg, P.E., Blieck, A., Blom, H., Clack, J.A., Poty, E. Thorez, J. and Janvier, P. (2004). Devonian tetrapod from western Europe. *Nature*, **427**, 412-413.

Compston, W. (2004). SIMS U-Pb zircon ages for the Upper Devonian Snobs Creek and Cerberean Volcanics from Victoria, with age uncertainty based on UO_2/UO v. UO/U precision. *Journal of the Geological Society, London* **161**, 223-228.

Denison, R.H. (1958). Early Devonian fishes from Utah. Part III. Arthrodira. *Fieldiana Geology* **11**, 357-458.

Denison, R.H. (1978). 'Placodermi. Handbook of Paleoichthyology, Volume 2'. (Ed. H.P. Schultze). (Gustav Fischer Verlag, Stuttgart, New York), 128 pp.

Draper, J.J. (1976). The Devonian rocks of the Toko Syncline, western Queensland. *Bureau of Mineral Resources, Australia, Record* **1976/29**, 16 pp.

Dupret, V. (2004). The phylogenetic relationships between actinolepids (Placodermi: Arthrodira) and other arthrodires (phlyctaeniids and brachythoracids). In 'Lower vertebrates from the Palaeozoic. First International Palaeontological Congress (IPC 2002), Sydney, Australia, July 2002. Proceedings of Symposium 6 (Palaeozoic Vertebrates)' (Ed. G. C. Young). *Fossils & Strata* **50**, 44-55.

Freeman, M.J. (1986). 'Huckitta SF53-11. 1:250 000 Geological Map Series. Explanatory Notes'. Northern Territory Geological Survey, 58 pp.

Gilbert-Tomlinson, J.G. (1968). A new record of *Bothriolepis* in the Northern Territory of Australia. *Bureau of Mineral Resources, Australia, Bulletin* **80**, 191-224.

Haines, P.W., Bagas, L., Wyche, S., Simons, B. and Morris, D.G. (1991). 'Barrow Creek SF53-6. 1:250 000 Geological Map Series Explanatory Notes'. Northern Territory Geological Survey, Darwin, 53 pp.

Hills, E.S. (1929). The geology and palaeontography of the Cathedral Range and Blue Hills in northwestern Gippsland. *Proceedings of the Royal Society of Victoria* **41**, 176-201.

Hills, E.S. (1931). The Upper Devonian fishes of Victoria, Australia, and their bearing on the stratigraphy of the state. *Geological Magazine* **68**, 206–231.

Hills, E.S. (1958). A brief review of Australian fossil vertebrates. In 'Studies on Fossil Vertebrates (Ed. T.S. Westoll) pp. 86-107 (Athlone Press, London).

Hills, E.S. (1959). Record of *Bothriolepis* and *Phyllolepis* (Upper Devonian) from the Northern Territory of Australia. *Journal and Proceedings of the Royal Society of New South Wales* **92**, 174-175.

Leriche, M. (1931). Les poissons Famenniens de la Belgique. *Académie Royale de Belgique, Mémoire* (Sér. 2) **10**, 1-72.

Lohest, M. (1888). Recherches sur les poissons des terrains paléozoïques de Belgique. Poissons des Psammites du Condroz, Famennien supérieur. *Annales de la Societé Géologique de Belgique* **15**, 112-203.

Long, J.A. (1984). New phyllolepids from Victoria, and the relationships of the group. *Proceedings of the Linnean Society of New South Wales* **107**, 263-308.

Long, J.A. (1989). Phyllolepid placoderms from the Late Devonian of eastern Victoria. In 'Pathways in Geology: Essays in Honour of Edwin Sherbon Hills' (Ed. R.W. Le Maitre) pp. 52-58 (Blackwell Scientific Publications, Melbourne).

Long, J.A. (1999). A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. *Records of the Western Australian Museum, Supplement* **57**, 37-53.

Mark-Kurik, E. (1973). *Actinolepis* (Arthrodira) from the Middle Devonian of Estonia. *Palaeontographica* **143A**, 89-108.

McCoy, F. (1848). On some new fossil fishes of the Carboniferous period. *Annals and Magazine of Natural History* **2**, 1-10.

Miles, R.S. (1971). The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of London. B. Biological Sciences* **263**, 101-234.

Rade, J. (1964). Upper Devonian fish from the Mount Jack area, New South Wales, Australia. *Journal of Paleontology* **38**, 929-932.

Ritchie, A. (1973). *Wuttagoonaspis* gen. nov., an unusual arthrodire from the Devonian of Western New South Wales, Australia. *Palaeontographica* **143A**, 58-72.

Ritchie, A. (1984). A new placoderm, *Placolepis* gen. nov. (Phyllolepidae) from the Late Devonian of New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales* **107**, 321–353.

Stensiö, E.A. (1934). On the Placodermi of the Upper Devonian of East Greenland. I. Phyllolepida and Arthrodira. *Meddelelser om Grønland*, **97(1)**, 1-58, 25 pl.

Stensiö, E.A. (1936). On the Placodermi of the Upper Devonian of East Greenland. Supplement to Part I. *Meddelelser om Grønland*, **97(2)**, 1-52, 30 pl.

Stensiö, E.A. (1939). On the Placodermi of the Upper Devonian of East Greenland. Second supplement to Part I. *Meddelelser om Grønland*, **97(3)**, 1-33, 6 pl.

Stidolph, P.A., Bagas, L., Donnellan, N., Whalley, A.M., Morris, D.G. and Simons, B. (1988). Elkedra SF53-7. 1:250 000 Geological Map Series Explanatory Notes. Northern Territory Geological Survey, Darwin, 54 pp.

Talent, J.A., Mawson, R., Aitchison, J.C., Becker, R.T., Bell, K.N., Bradshaw, M.A., Burrow, C.J., Cook, A.G., Dargan, G.M., Douglas, J.G., Edgecombe, G.D., Feist, M., Jones, P.J., Long, J.A., Phillips-Ross, J.R., Pickett, J.W., Playford, G., Rickards, R.B., Webby, B.D., Winchester-Seeto, T., Wright, A.J., Young, G.C. and Zhen, Y.-Y. (2000). Devonian palaeobiogeography of Australia and adjoining regions. In 'Palaeobiogeography of Australasian Faunas and Floras' (Eds. A.J. Wright, G.C. Young and J.A. Talent) *Association of Australasian Palaeontologists, Memoir* **23**, 167-257.

Young, G.C. (1974). Stratigraphic occurrence of some placoderm fishes in the Middle and Late Devonian. *Newsletters on Stratigraphy* **3**, 243-261.

Young, G.C. (1980). A new Early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. *Palaeontographica* **167A**, 10-76, 27 text-figs., 2 pls.

Young, G.C. (1985). New discoveries of Devonian vertebrates from the Amadeus Basin, central Australia. *BMR Journal of Australian Geology & Geophysics* **9**, 239-254.

Young, G.C. (1988). New occurrences of phyllolepid placoderms from the Devonian of central Australia. *BMR Journal of Australian Geology & Geophysics* **10**, 363-376.

Young, G.C. (1989). The Aztec fish fauna of southern Victoria Land - evolutionary and biogeographic significance. In 'Origins and Evolution of the Antarctic Biota' (Ed. J.A. Crame), *Geological Society of London Special Publication* **47**, 43-62.

Young, G.C. (1990). Devonian vertebrate distribution patterns, and cladistic analysis of palaeogeographic hypotheses. In 'Palaeozoic biogeography and palaeogeography' (Eds. W.S. McKerrow and C.R. Scotese). *Geological Society of London Memoir* **12**, 243-255.

Young, G.C. (1993a). Middle Palaeozoic macrovertebrate biostratigraphy of Eastern Gondwana. In 'Palaeozoic Vertebrate Biostratigraphy and Biogeography'. (Ed. J.A. Long). 208-251. (Belhaven Press, London).

Young, G.C. (1993b). Vertebrate faunal provinces in the Middle Palaeozoic. In 'Palaeozoic Vertebrate Biostratigraphy and Biogeography'. (Ed. J.A. Long) 293-323. (Belhaven Press, London).

Young, G.C. (1996). Devonian (chart 4). In 'An Australian Phanerozoic Timescale' (Eds. G.C. Young and J.R. Laurie). 96-109. (Oxford University Press, Melbourne).

Young, G.C. (1999). Preliminary report on the biostratigraphy of new placoderm discoveries in the Hervey Group (Upper Devonian) of central New South Wales. *Records of the Western Australian Museum, Supplement* **57**, 139–150.

Young, G.C. (2003). North Gondwanan mid-Palaeozoic connections with Euramerica and Asia; Devonian vertebrate evidence. *Courier Forschungsinstitut Senckenberg* **242**, 169-185.

Young, G.C. (in press a). An articulated phyllolepid fish (Placodermi) from the Devonian of central Australia: implications for non-marine connections with the Old Red Sandstone continent. *Geological Magazine* [accepted].

Young, G.C. (in press b). New phyllolepids (placoderm fishes) from the Middle-Late Devonian of southeastern Australia. *Journal of Vertebrate Paleontology* [accepted].

Young, G.C. and Goujet, D. (2003). Devonian fish remains from the Dulcie Sandstone and Cravens Peak Beds. Georgina Basin, central Australia. *Records of the Western Australian Museum, Supplement* **65**, 85 pp., 42 figures.

Young, G.C., and Long, J.A. (submitted). Phyllolepid placoderm fish remains from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Antarctic Science* [in review].

Young, G.C. and Turner, S. (2000). Devonian microvertebrates and marine-nonmarine correlation in East Gondwana: Overview. *Courier Forschungsinstitut Senckenberg* **223**, 453-470.